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## **Mediterranean small mammals and insular syndrome: Biometrical study of the long-tailed field mouse (*Apodemus sylvaticus*) (Rodentia-Muridae) of Corsica**

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**Abstract.** The presence in Corsica of a field mouse is well known. Several authors have noted some of its morphological peculiarities but it was only recently (1980) that the presence of *A. sylvaticus* was established with certainty. However, this evidence is based on a check of a limited number of individuals originating from a single locality. In order to generalize these observations, we performed a biochemical test on six Corsican mice caught in three distinct localities and a morpho-biometrical study of 491 skulls. The results show that *A. sylvaticus* is spread all over the island and that *A. flavicollis* is probably absent. No sexual dimorphism was found but strong spatial variations in the cranial measurements were evidenced. These are far less important between the various Corsican sub-samples than between the insular and the continental mice. The evolutionary and adaptive significance of the increase in size of insular mice is discussed in relation to the theory of island biogeography and to the present knowledge on the history of the mammalian settlement of the island.

**Key words.** Mammalia, Muridae, *Apodemus*, Corsica, insular syndrome, competition, evolution, size increase.

### **Introduction**

For many insular communities, the so called “insularity syndrome” (Blondel 1986) involves a set of evolutionary changes affecting these communities when compared to continental ones i. e. less species, a wider ecological niche, a lower predation pressure and some phenotypical changes (general morphology, increase in size . . .).

The changes of the width of the niche observed in insular rodents are generally interpreted as a consequence of the weakening of the competitive interactions and of a lower predation pressure. Furthermore, a reduction of the capabilities of spreading is observed (Crowell 1973, Sullivan 1977, Tamarin 1977) as well as population density changes (increase: Sullivan 1977, Tamarin 1977, Gliwicz 1980, Crowell 1983, Adler et al. 1986, Granjon & Cheylan 1988, decrease: Delany 1970, Adler & Tamarin 1984), a reduction of the aggressivity (Halpin & Sullivan 1978), and alterations of demographic or social characteristics (Gliwicz 1980)). These modifications lead the insular populations towards a «k-selected» demographic strategy (Berry & Jakobson 1975, Tamarin 1978).

Taking previous works (Wilson 1961, Carlquist 1966) into account, Macarthur & Wilson (1967) defined a “taxon cycle” comprising three successive phases of the evolution of insular communities: a. invasion of secondary habitats (low successional stages: open, unpredictable or degraded habitats) by «r-selected» species; b. occupation of primary habitats (forests) leading to a weakening of the dispersal

capabilities and progressively towards «k-selected» demographic traits; c. differentiation and even speciation.

These authors point out the role of the interspecific competition which drives the first colonizing species into the forested habitats and leads to a high degree of isolation and finally to a distinct evolution.

Though several authors have had some reservations about the importance of competition (Connell 1983, Schoener 1983, Bradley & Bradley 1985) many examples confirm the merits of that hypothesis at least in birds and reptiles (Brown & Gibson 1983, Pacala & Roughgarden 1985, Rummel & Roughgarden 1985). As far as mammals are concerned, some observations dealing with insular rodent communities lead to the same conclusions (Grant 1972, Crowell 1973 and 1983, Crowell & Pimm 1976, Hallett 1982, Hallett et al. 1983, Dueser & Porter 1986, Granjon & Cheylan 1988).

So, in insular communities, the isolation and the decrease of the interspecific competition can provide the required conditions for a geographical differentiation of the species or even for a rapid speciation involving selective mechanisms or stochastic effects.

The present contribution will discuss the various hypotheses related to the evolution of wild populations living in insular conditions by examining the Corsican wood mouse skull morphological variability.

Despite several morphological studies (Kahmann 1969, Pasquier 1974, Darviche 1978) and a general revision of the genus *Apodemus* throughout France (Saint Girons 1966 and 1967), the taxonomic status of the Corsican field mouse remained unclear for a long time.

Kahmann (1969) has shown that Corsican and Sardinian field mice generally have a fifth root on their first upper molar. In this regard, these animals differ considerably from the existing continental populations of *A. sylvaticus* and of *A. flavicollis*. Kahmann, however, did not decide on the taxonomic position of these insular mice. Filipucci (1987) found that the Sardinian wood mice were genetically very close to those from Elba and that these Tyrrhenian mice were closely related to those from the Italian peninsula. However, extending these observations to the Corsican mice is difficult since she has no samples from Corsica nor from Southern France for comparison.

Other studies have shown that in many regards (e. g. tail, hind foot and head and body length, most of the skull dimensions) the Corsican mice are significantly larger than continental *sylvaticus* and smaller than *flavicollis* (Darviche 1978, Orsini & Cheylan 1988, Libois & Fons 1990).

To which species do they belong? The first unquestionable evidence of the presence of *A. sylvaticus* in Corsica was given by Benmehdi et al. (1979) who made electrophoretical comparisons between Corsican mice and continental samples comprising individuals belonging to both *Apodemus* species. Nevertheless, we have to keep in mind that this fact does not exclude the eventual presence of the second species on the island: the mice studied in this way were indeed few and originated from the same locality (Manso).

The present study is an attempt to generalize these observations and to examine the extent of the morphometrical variability of the Corsican wood mouse.

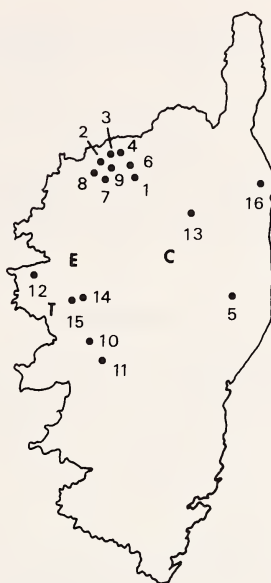


Fig. 1: Sample localities of mice in Corsica. Number of individuals in parentheses.

Live-trapped mice: C: Corti (1); E: Evisa (4); T: Tiuccia (1).

Skulls: 1 Olmi-Capella (50); 2 Cateri (92); 3 San Antonino (6); 4 Santa Reparata (15); 5 Pan-cheraccia (62); 6 Ville di Paraso (67); 7 Zilia (34); 8 Montemaggiore (67); 9 Avapessa (6); 10 Sarrola-Carcopino (29); 11 Cuttoli-Curticchiato (1); 12 Piana (3); 13 Aïti (2); 14 Murzu (1); 15 Vico (53); 16 La Canonica (3).

## Material

Mice skulls ( $n = 491$ ) were extracted from barn owl pellets collected in towers, churches and old houses all over the northern part of Corsica during the years 1980 and 1981 (Fig. 1).

On the mainland, we also collected barn owl pellets in Viens (Vaucluse;  $n = 49$ ) and Belflou (Aude;  $n = 35$ ) to sample Mediterranean populations of *A. sylvaticus*. To compare all that material with the nominal subspecies and with *A. flavicollis*, we made similar sampling in several localities of Belgium spread in the provinces of Liège, Luxembourg and Namur. The specific identity of these skulls was ascertained using the discriminant functions computed by Van der Straeten & Van der Straeten-Harrie (1977). Sample size is 47 for *A. s. sylvaticus* and 86 for *A. flavicollis*.

During the spring 1981, six Corsican mice were live trapped in three different localities. They were kept in captivity for further blood analyses. In the same way, we caught three *A. flavicollis* and two *A. sylvaticus* in the forests of Florenville (South Belgium).

## Methods

### Biochemistry

Blood samples were taken by retroorbital puncture and the blood treated as described in Debrot & Mermod (1977). An electrophoresis of serum albumins was performed on an agarose gel ( $20 \text{ Vcm}^{-1}$ ) and the proteins stained with Coomassie blue.

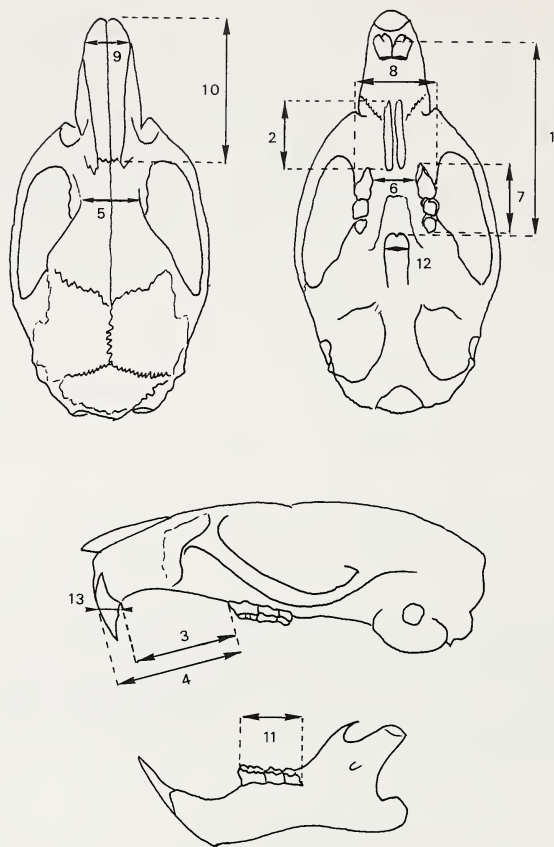


Fig. 2: Schematic view of a mouse skull. 1 Length Prosthion-Palation, 2 Length of foramen incisivum, 3 Length of diastema, 4 Length Incisor-M1, 5 Least Interorbital Constriction, 6 Width of palate at M1, 7 Length of upper molar row, 8 Width of dental arch, 9 Width of nasals, 10 Length of nasals, 11 Length of lower molar row, 12 Width of choana, 13 Depth of incisor.

### Morphology

The 13 skull measurements taken are shown in fig. 2. The precision (to the nearest 1/20th mm) was determined under a binocular lens. The skulls were sorted in age classes according to the criteria defined by Felten (1952). When a mouse skull was recovered alone in a pellet and associated with one pelvic girdle, the sex of the mouse was determined following the method described by Brown & Twigg (1969).

The number of the roots of the M<sup>1</sup> and the presence of a well developed t9 on the M<sup>2</sup> were also scored.

### Statistics

Simple statistics (mean, standard deviation, variation coefficient) were calculated for all the variables, by sex, age class or locality group. One and two-way analyses of variance were performed to check the origin of the variability in the data set. These F-tests were completed by

a principal component analysis dealing with 12 out of the variables (Nr 11 has been rejected). All the calculations were performed using the software Biomeco (Groupe Biométrie 1988).

## Results

### Biochemistry

The electrophoretic pattern of the six Corsican mice studied is very similar to that of the Belgian *sylvaticus* (only one spot) and differs from the *flavicollis* pattern (two spots).

### Morphology

The presence of a fifth root on the M<sup>1</sup> was observed in a very high number of the Corsican mice as compared with those from Belgium (Table 1). The  $X^2$  value (271.9) is very highly significant. There is, however, a strong similarity between the Belgian *sylvaticus* and *flavicollis* samples ( $X^2 = 0.0037$ ;  $p < 0.05$ ) and a slight, though non-significant, difference ( $X^2_{\text{corr}} = 2.45$ ;  $p > 0.05$ ) between both mainland forms of *A. sylvaticus*.

No difference was found between males and females ( $X^2 = 0.0086$ , N. S.) in Corsica nor between age classes in Belgium ( $X^2_{\text{corr}} = 0.832$ , N. S. and  $X^2_{\text{corr}} = 0.896$ , N. S. respectively for *sylvaticus* and for *flavicollis*). In Corsica, the frequency of a fifth root on the M<sup>1</sup> seems to be somewhat lower in the oldest mice (age class 5) ( $X^2_{\text{corr}} = 9.32$ ,  $p \approx 0.025$ ).

We also found strong differences related to the localities in the fifth root frequency ( $X^2 = 32.73$ ,  $p < 0.001$ ). That frequency is significantly lower in the localities 1 and

Table 1: Number of roots on the first upper molar.

| Root number                | 4  | 5   |
|----------------------------|----|-----|
| Belgium <i>flavicollis</i> | 71 | 15  |
| Belgium <i>sylvaticus</i>  | 39 | 8   |
| France <i>sylvaticus</i>   | 42 | 2   |
| Corsica Total              | 85 | 402 |
| males                      | 13 | 43  |
| females                    | 11 | 38  |
| age class 2                | 3  | 15  |
| age class 3                | 15 | 128 |
| age class 4                | 42 | 200 |
| age class 5                | 21 | 55  |
| locality 1                 | 13 | 37  |
| locality 2                 | 28 | 64  |
| locality 5                 | 13 | 49  |
| locality 6                 | 4  | 63  |
| locality 7                 | 2  | 32  |
| locality 8                 | 5  | 60  |
| locality 10                | 4  | 25  |
| locality 15                | 4  | 49  |

Table 2: Presence of a well developed t9 on the second upper molar. (\* not well developed but present)

|                            | no  | yes |
|----------------------------|-----|-----|
| Belgium <i>sylvaticus</i>  | 0   | 36  |
| Belgium <i>flavicollis</i> | 28  | 9   |
| Corsica                    | 24* | 239 |
| Southern France            | 6   | 38  |

2 (72.1 %) than in the samples 6, 7, 8 and 15 (93.2 %). The localities 5 and 10 show an intermediate value (81.3 %).

As the presence of a well developed t<sup>9</sup> on the second upper molar is concerned, we found no frequency difference between the Corsican mice and the mainland *sylvaticus* ones ( $X^2 = 4.81$ , N. S.) (Table 2). The difference is highly significant when *flavicollis* is considered ( $X^2 = 118.60$ ,  $p < 0.001$ ).

### Biometry

Simple statistics (mean, variance and variation coefficient) are presented in table 3. Note that we found no statistical difference between the two samples of mice collected in southern France except for V8. These two samples were thus pooled in the further calculations. Considering the whole Corsican data set, all the frequency distributions of the skull measurements show only a single mode. Though of the same order of magnitude, the variation coefficient is generally lower in the Corsican mice than in the others and except in a few cases (variables 5, 8 and 12), the values of the means for the Corsican mice fall between those of *A. flavicollis* and the mainland *A. sylvaticus*. Student's t-tests were performed between the Corsican mice and the other samples. All the t values are significant at least at the 0.05 level except for V.6, V.12 and V.13 in the comparisons between the Corsican and the mainland French mice and for V.4, V.9 and V.10 between the two mainland *sylvaticus* samples.

**Sexual dimorphism:** We found no difference between males and females except for the diastema length and the choana width which are slightly greater in males (Student's t-test significant respectively at the 0.02 and 0.04 levels). The one-way F-tests performed for each variable show no significant difference between the sexes. When the interaction with the age or the locality is considered (two-way ANOVA), the influence of the sex on the total variability of the data is rejected in all the cases (F values are never significant). The global F values taking into account the interaction between the sex and the age on the one hand, and between the sex and the locality on the other hand, are also not significant in all the cases but one (palatal width).

**Variability due to the age:** When the age is considered alone, all the computed F values (4 age classes) are highly ( $p < 0.0005$ ) significant with only four exceptions: the palatal width ( $p = 0.01$ ), the choana width and the length of both (upper and lower) molar rows (not significant).

The age group means of these ten skull dimensions showing significant age-variations, can be ranked in the following order: class 2 < class 3 < class 4 < class 5.

Table 3: Statistical description of *Apodemus* samples (n: number of observations, m: mean, s2: variance, cv: coefficient of variation).

| Samples<br>Var. |    | Corsica | France | Belgium           |                    |
|-----------------|----|---------|--------|-------------------|--------------------|
|                 |    |         |        | <i>sylvaticus</i> | <i>flavicollis</i> |
| V1              | n  | 446     | 78     | 47                | 82                 |
|                 | m  | 11.42   | 11.17  | 10.63             | 11.99              |
|                 | s2 | 0.14    | 0.28   | 0.23              | 0.38               |
|                 | CV | 3.29    | 4.74   | 4.48              | 5.15               |
| V2              | n  | 470     | 82     | 47                | 86                 |
|                 | m  | 5.62    | 5.24   | 5.40              | 5.54               |
|                 | s2 | 0.08    | 0.13   | 0.10              | 0.10               |
|                 | CV | 5.07    | 6.88   | 5.94              | 5.82               |
| V3              | n  | 470     | 82     | 47                | 86                 |
|                 | m  | 6.88    | 6.28   | 6.53              | 7.29               |
|                 | s2 | 0.09    | 0.15   | 0.14              | 0.18               |
|                 | CV | 4.33    | 6.17   | 5.79              | 5.75               |
| V4              | n  | 470     | 82     | 47                | 85                 |
|                 | m  | 7.78    | 7.26   | 7.41              | 8.44               |
|                 | s2 | 0.11    | 0.19   | 0.20              | 0.31               |
|                 | CV | 4.30    | 6.02   | 6.01              | 6.63               |
| V5              | n  | 482     | 82     | 47                | 86                 |
|                 | m  | 4.22    | 4.01   | 3.90              | 4.17               |
|                 | s2 | 0.02    | 0.03   | 0.04              | 0.03               |
|                 | CV | 3.44    | 4.24   | 4.80              | 4.06               |
| V6              | n  | 448     | 70     | 47                | 41                 |
|                 | m  | 2.70    | 2.74   | 2.62              | 2.77               |
|                 | s2 | 0.04    | 0.02   | 0.05              | 0.03               |
|                 | CV | 7.03    | 5.18   | 8.46              | 6.12               |
| V7              | n  | 465     | 81     | 47                | 53                 |
|                 | m  | 3.83    | 3.69   | 3.59              | 3.93               |
|                 | s2 | 0.01    | 0.04   | 0.02              | 0.03               |
|                 | CV | 3.13    | 5.57   | 4.19              | 4.67               |
| V8              | n  | 435     | 70     | 47                | 41                 |
|                 | m  | 5.10    | 5.20   | 4.81              | 5.04               |
|                 | s2 | 0.04    | 0.03   | 0.03              | 0.03               |
|                 | CV | 3.78    | 3.21   | 3.55              | 3.47               |
| V9              | n  | 440     | 53     | 47                | 80                 |
|                 | m  | 2.98    | 2.79   | 2.82              | 3.17               |
|                 | s2 | 0.04    | 0.04   | 0.04              | 0.05               |
|                 | CV | 6.97    | 7.46   | 6.88              | 7.14               |
| V10             | n  | 439     | 53     | 47                | 78                 |
|                 | m  | 9.55    | 8.76   | 8.70              | 9.91               |
|                 | s2 | 0.25    | 0.23   | 0.29              | 0.42               |
|                 | CV | 5.28    | 5.50   | 6.17              | 6.53               |
| V11             | n  | 80      | 80     | —                 | —                  |
|                 | m  | 3.90    | 3.75   |                   |                    |
|                 | s2 | 0.04    | 0.03   |                   |                    |
|                 | CV | 5.13    | 4.80   |                   |                    |
| V12             | n  | 425     | 78     | 47                | 78                 |
|                 | m  | 0.95    | 0.98   | 0.89              | 0.90               |
|                 | s2 | 0.03    | 0.02   | 0.03              | 0.03               |
|                 | CV | 18.59   | 13.94  | 17.80             | 18.01              |
| V13             | n  | 484     | 82     | 47                | 84                 |
|                 | m  | 1.22    | 1.23   | 1.15              | 1.39               |
|                 | s2 | 0.005   | 0.006  | 0.007             | 0.010              |
|                 | CV | 5.55    | 6.26   | 7.24              | 7.03               |

Table 4: Two-way (locality/age class) analysis of the variance. Signification levels of the F values. Age classes 3, 4 and 5 and localities 1, 2, 5, 6, 7, 8 and 15 are always included except for V11 (only localities 1 and 4). Locality 10 has been added for V6.

| Variable | Source of variation |           |          |
|----------|---------------------|-----------|----------|
|          | interaction         | age class | locality |
| V 1      | <0.0005             | <0.005    | <0.01    |
| V 2      | <0.0005             | ≈0.005    | N. S.    |
| V 3      | <0.0005             | <0.005    | ≈0.01    |
| V 4      | <0.0005             | <0.001    | N. S.    |
| V 5      | ≈0.0005             | ≈0.006    | <0.0005  |
| V 6      | =0.025              | N. S.     | <0.0005  |
| V 7      | N. S.               | N. S.     | ≈0.03    |
| V 8      | <0.0005             | <0.025    | <0.0005  |
| V 9      | <0.0005             | <0.005    | <0.0005  |
| V 10     | <0.0005             | <0.005    | ≈0.005   |
| V 11     | N. S.               | N. S.     | N. S.    |
| V 12     | <0.05               | N. S.     | <0.01    |
| V 13     | <0.0005             | <0.005    | N. S.    |



Fig. 3: Factor loadings of the skull dimensions on the two first principal components. Variable numbers are the same as in fig. 2.

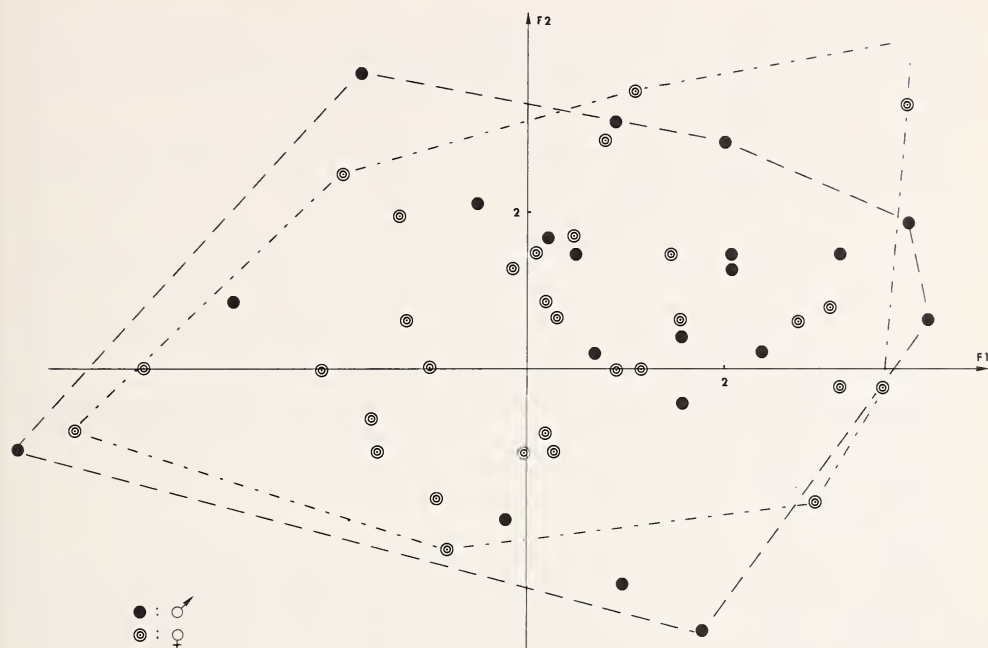


Fig. 4: Scattergram of the male and female Corsican field mice in the space of the two first principal components (F1 & F2).

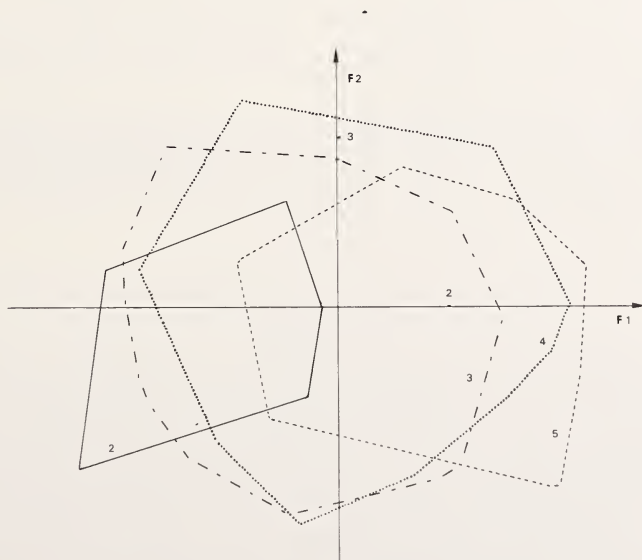


Fig. 5: Scattergram of the clouds of four age groups of Corsican field mice in the space F1 X F2. Age class numbers as in Felten (1952).

**Stational variability:** The F tests performed to compare the samples originating from different localities in Corsica are highly significant ( $p < 0.01$  except in V.4, where  $p < 0.05$ ), suggesting that there are strong stational differences for all the studied skull dimensions.

Taking into consideration the interaction between the age class and the locality, we obtained the results of table 4 where the locality appears as a main source of variation in all but four variables.

**Principal Component Analysis:** The part of the total variability extracted by the principal axes is 45.2 % on F1; 12.3 % on F2; 7.6 % on F3 and 6.9 % on F4.

Since all the variables but one (choana width) are positively correlated to the F1 axis, F1 must be considered as a size axis. F2 is rather a shape axis because some of the variables are positively and some others negatively correlated to it.

Consequently, the bigger a mouse is, the more distant to the right of the diagram it lies. Along the F2 axis, the mice with a thinner and longer rostrum are positively correlated in contrast to those with a broader palate (Fig. 3).

In fig. 4, the total overlap between the male and female clusters of Corsican mice appears clearly.

In fig. 5, it can be seen that the age clusters rank according to growth.

As far as local variations are concerned, fig. 6 shows slight differences between the samples, sample 1 comprising many of the biggest mice with a thin and long muzzle. Nevertheless, the overlap between all these samples is by far much more important than the overlap between the "global" Corsican cluster and the mainland *sylvaticus* ones, on the one hand, and between the same Corsican cluster and the *flavicollis* one, on the other hand (Fig. 7). The minor differences between the two mainland populations of *sylvaticus* are also worth to be mentioned.

In order to specify the meaning of these variations, we computed the Coefficient of Difference of Mayr et al. (1953)  $[(\text{mean}_1 - \text{mean}_2)/(\text{std}_1 + \text{std}_2)]$  between the adult individuals (age class 4) of the samples 1, 2, 5, 6, 7, 8 and 15. It was performed for all the variables with the exception of V.11.

The highest values of that coefficient are observed between both species of *Apodemus* or between the Corsican mice and the continental populations of either species. It is worthwhile to notice that two CD values involving only Corsican samples are of the same importance (Table 5).

## Discussion

From biochemical and morphological studies we can see that the seralbumins of the Corsican mice are of the *sylvaticus* type and that their second upper molar does not lack a ninth cusp as is the case in *A. flavicollis*. In some cases, however, the t9 is reduced in size but this is also true for continental *sylvaticus* populations (Michaux 1990). Both these characters being discriminative between *A. flavicollis* and *A. sylvaticus* (Pasquier 1974, Debrot & Mermod 1977), we can conclude that the long-tailed field mouse of Corsica belongs to the *sylvaticus* species. If *A. flavicollis* were present and relatively abundant in Corsica, we should have observed a bimodality in the frequency distribution of some morphometrical variables and the Corsican

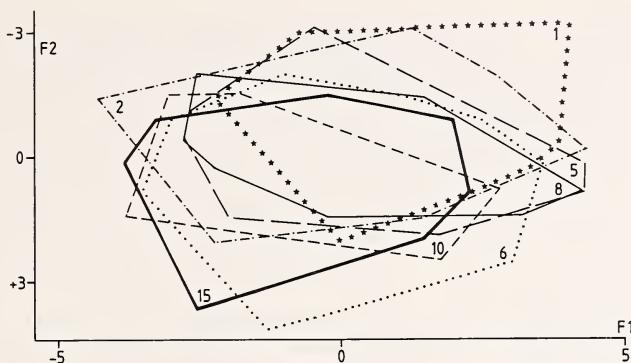


Fig. 6: Scattergram of the clusters of different Corsican field mice samples in the space F1 X F2. Sample numbers as in fig. 1.

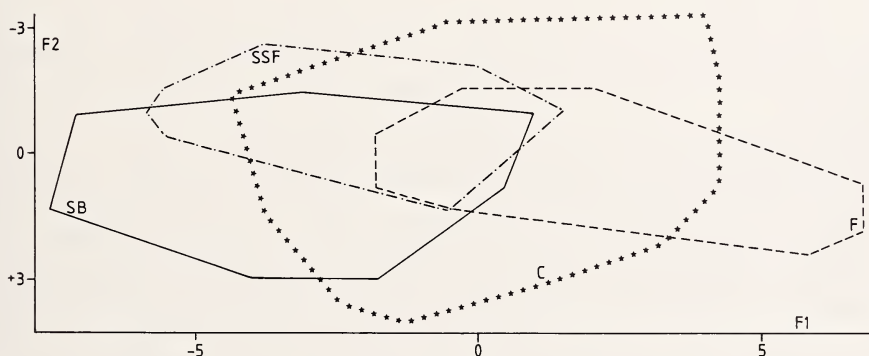


Fig. 7: Scattergram of the clusters of the four studied taxa of field mouse. C: *Apodemus* from Corsica; F: *A. flavicollis* from Belgium; SB: *A. s. sylvaticus* from Belgium; SSF: *A. sylvaticus dichrurus* (?) from Southern France.

cluster (P. C. A.) should have been less compact and less regular in shape. Thus, the probability of *A. flavicollis* being present on the island is low.

Nevertheless, Corsican mice are quite different from the continental subspecies, namely by having a fifth root on their first upper molar. That character is shared with Sardinian mice which are also very similar to them in so far as other dental characters are considered (Michaux 1990). Unfortunately, we lack some comparisons between Corsican and Italian samples (insular and continental). Further studies are thus needed before drawing any conclusion about the subspecific status of the Corsican field mouse.

The absence of a sexual dimorphism in the skull dimensions of the Corsican field mouse confirms what has been observed in other populations (e. g. Hedges 1969, Van der Straeten & Van der Straeten-Harrie 1977, Ramalhinho & Madureira 1982).

Table 5: Variables showing the highest values of the Coefficient of Difference (C. D.) in paired comparisons. C. D. =  $(\text{mean}(A) - \text{mean}(B)) / (\text{std}(A) + \text{std}(B))$ .

|                                      | Levels | <i>Apodemus flavicollis</i> | <i>Apodemus sylvaticus</i> (Belgium) | 1          | 2      | 5      | Corsican samples |  |     | 7           | 8    | 15  |
|--------------------------------------|--------|-----------------------------|--------------------------------------|------------|--------|--------|------------------|--|-----|-------------|------|-----|
| <i>Apodemus flavicollis</i>          | A      |                             | V7, V13                              |            |        | V13    | V13              |  | V13 |             |      | V13 |
|                                      | B      |                             | V1, V3                               | V13        | V13    |        |                  |  |     |             | V13  |     |
|                                      | C      |                             | V8                                   |            |        |        |                  |  |     | V4          |      |     |
| <i>Apodemus sylvaticus</i> (Belgium) | A      |                             |                                      | V1, V3, V8 |        | V7, V8 |                  |  | V7  | V7, V8      |      | V7  |
|                                      | B      |                             |                                      | V7         |        |        | V7               |  |     |             |      | V8  |
|                                      | C      |                             |                                      | V10        | V1, V8 | V1, V5 | V1               |  | V1  | V1, V5, V10 |      |     |
| <i>Apodemus sylvaticus</i> (France)  | A      | V3, V4                      | V8                                   | V3         |        | V3     |                  |  |     |             |      |     |
|                                      | B      | V10, V13                    |                                      | V10        |        | V10    |                  |  |     |             | V 10 |     |
|                                      | C      | V9                          |                                      |            | V3     | V5     | V3               |  |     | V3, V5      |      |     |
| Corsica sample 1                     | A      |                             |                                      |            | V2     |        |                  |  |     |             |      |     |
|                                      | C      |                             |                                      |            |        |        | V3               |  |     |             |      |     |

Level A: C. D. &gt;1.0: 15 % of A individuals overlap 15 % of B individuals

Level B: C. D. &gt;0.9: 18 % of A individuals overlap 18 % of B individuals

Level C: C. D. &gt;0.8: 21 % of A individuals overlap 21 % of B individuals (after Gery, 1962)

The differences between age classes are not surprising. They are undoubtedly related to growth processes and account for a significant part of the observed variability.

Another important source of variability is a "geographical" one. Indeed, we observed some differences between samples collected in various localities. Generally, these differences are statistically significant but slight. The mice of sample 1 and, to a lesser extent, those of sample 2, however, seem to be rather distinct from the others: they are bigger and the frequency of a fifth root on the M<sup>1</sup> is lower in both these samples than in all the others. These differences in size still cannot be satisfactorily explained. Since sample 1 has been collected in Olmi Capella, the most elevated village of our research area, it can be suggested, as a hypothesis, that they should be related to altitude (Bergmann's rule). They could also be the consequence of a lower competition with the black rat and the house mouse whose density decreases with rising altitude (Libois 1984).

A point to highlight is the general increase in skull size of the Corsican mice. As compared with the other Corsican rodent species (black rat, house mouse and garden dormouse), the wood mouse shows the greater morphological differences in respect to continental populations (Orsini & Cheylan 1988).

That fact must be emphasized more especially as, all over South-West Europe, the recent and fossil wood mice of the *sylvaticus-flavicollis* group have remained phenotypically remarkably stable throughout the last three million years (Pasquier 1974, Michaux 1983). In continental Europe, there is a clear size and weight increase in south-western *sylvaticus* populations compared to more eastern or northern ones, which are sympatric with *A. flavicollis* (Ursin 1956, Alcantara 1991). In Israël, Tchernov (1979) has shown that during the Middle and Upper Pleistocene, the size of *A. sylvaticus* was strongly affected independently of climate, becoming larger in the absence of its competitor, *A. flavicollis*. Corsican mice, however, are far more larger than continental ones belonging to allopatric populations (Libois & Fons 1990; this

study). Following Angerbjörn (1986), a size increase seems rather general in island populations of that species, mainly on the smaller islands, (i. e., for the west Mediterranean realm: Pantelleria: Felten & Storch 1970; Elba: Kahmann & Niethammer 1971; Formentera: Sans-Coma & Kahmann 1977; Porquerolles: Libois & Fons 1990). Angerbjörn thinks that it is induced by a weakening of the interspecific competition and by a reduction of the predation pressure in insular conditions: less competitors and less predators could allow an enlargement of the trophic niche of the mouse which can take advantage of a greater size in exploiting more diversified food resources. Could this be the case in Corsica?

As quoted by many authors (Macarthur & Wilson 1967, Blondel 1986, Williamson 1981) the depletion of the number of insular species is somewhat balanced by a population density increase of these species and by a widening of their ecological niche.

In Corsica, the number of mammalian species is reduced to 38 % when compared with similar continental areas. Considering the three Corsican murid species, it appears that the densities of both the black rat and the house mouse are higher on the island than in similar continental habitats. This is not the case for the wood mouse (Orsini 1982; Cassaing & Croset 1985, Boitani et al. 1985, Cheylan 1986). Similar observations were made by Libois (1984) about the habitat width of these three species. The insular density increase and the widening of the ecological niche are generally thought to be a consequence of a decrease of predation pressure and of interspecific competition (Lidicker 1973, Tamarin 1977, Cheylan & Granjon 1985).

Assuming that the predation pressure on the wood mouse and on the house mouse is of a similar level, since their body size is nearly the same, the fact that no density or habitat width increase is observed in the wood mouse populations could be linked with the persistence of the interspecific competition.

From the history of murid settlement in Corsica, we can see that during the Pleistocene and at the beginning of the Holocene, only two rodent species were living in Corsica: *Rhagamys orthodon* (Muridae) and *Tyrrhenicola henseli* (Microtidae). They vanished at the end of the first millennium B. C. (Vigne 1983a, b). Whereas the oldest remains of the black rat (*Rattus rattus*) trace back to the VIth century B. C. (Vigne & Marinval-Vigne 1985) and no fossil remains of *Mus* have ever been found in Corsica, it is established that the wood mouse did appear on the island at the beginning of the third millennium B. C. and did coexist there with the two endemic rodents. Nevertheless, its skull remains are far less numerous than those of *Rhagamys* and of *Tyrrhenicola*, at least until the end of the first millennium B. C. (Vigne 1983b). Taking into account the larger size of *Rhagamys* and *Tyrrhenicola* (nearly 50 g, Michaux, pers. comm. in Granjon & Cheylan 1988), could we assume that, in syntopic conditions, the wood mouse was dominated and that its spread all over the island was slowed down? The very rapid and simultaneous disappearance of both endemic rodents corresponds to the Europe-wide spread of the black rat (Armitage et al. 1984) and to the arrival of that latter species in Corsica. Vigne & Marinval-Vigne (1991) think that this event could be the main reason explaining the extinction of the endemic rodents.

As soon as it was present on the island, the wood mouse faced important competitive pressure from the other larger rodents. For ecological reasons, it is however most unlikely that the thermophilic black rat and house mouse, could quickly reach cool climate forests and mountain habitats where the wood mouse and the dormice (*Glis glis* and *Eliomys quercinus*) live. Consequently, the wood mouse is the only species belonging to the Corsican murid guild which is able to colonize the middle-mountain forest habitats where the interspecific competition is weakened.

### Conclusions

First, our results confirm that the Corsican long-tailed field mouse belongs to *Apodemus sylvaticus*.

Secondly, they show that this mouse differs significantly from continental populations of the same species, namely in respect to skull size. However, the question of a distinct subspecific rank for the Corsican mouse remains open: more data about other Mediterranean insular and continental populations are needed before drawing a general conclusion on this point.

Thirdly, they reinforce the idea that the increase in size seems to be a general pattern of adaptation of the species to insular conditions (less interspecific competition) and not an effect of any genetic drift.

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### References

- Adler, G. H. & R. H. Tamarin (1984): Demography and reproduction in island and mainland white-footed mice (*Peromyscus leucopus*) in southeastern Massachusetts. — *Can. J. Zool.* 62: 58–64.
- Adler, G. H., M. L. Wilson & M. J. Deroose (1986): Influence of island area and isolation on population characteristics of *Peromyscus leucopus*. — *J. Mammal.* 67: 406–409.
- Alcantara, M. (1991): Geographical variation in body size of the Wood Mouse *Apodemus sylvaticus*. — *Mammal Review* 21: 143–150.
- Angerbjörn, A. (1986): Gigantism in island populations of wood mice (*Apodemus*) in Europe. — *Oikos* 47: 47–56.
- Armitage, P., B. West & K. Steedman (1984): New evidence of black rat in Roman London. — *London Archaeologist* 4: 375–383.
- Benmehdi, F., J. Britton-Davidian & L. Thaler (1980): Premier rapport de la génétique biochimique des populations à la systématique des mulots de France continentale et de Corse. — *Bioch. Syst. Ecol.* 8: 309–315.
- Berry, R. J. & M. E. Jakobson (1975): Ecological genetics of an island population of the house mouse (*Mus musculus*). — *J. Zool. Lond.* 175: 523–540.
- Blondel, J. (1986): Biogéographie évolutive. — Paris, Masson.
- Boitani, L., A. Loy & P. Molinari (1985): Temporal and spatial displacement of two rodents (*Apodemus sylvaticus* and *Mus musculus*) in a mediterranean coastal habitat. — *Oikos* 45: 246–252.
- Bradley, R. A. & D. V. Bradley (1985): Do non-random patterns of species in niche space imply competition? — *Oikos* 45: 443–445.

- Brown, J. C. & G. I. Twigg (1969): Studies on the pelvis in British Muridae and Cricetidae (*Rodentia*). — J. Zool. Lond. 158: 81–132.
- Brown, J. H. & A. C. Gibson (1983): Biogeography. — C. V. Mosby company.
- Carlquist, S. (1986): Loss of dispersability in Pacific Compositae. — *Evolution* 20: 30–48.
- Cassaing, J. & H. Croset (1985): Organisation spatiale, compétition et dynamique des populations sauvages de souris (*Mus spretus* et *Mus musculus*) du midi de la France. — *Z. Säugetierk.* 50: 271–284.
- Cheylan, G. (1986): Facteurs historiques, écologiques et génétiques de l'évolution des populations méditerranéennes de *Rattus rattus* (L.). — Thèse. Doct. Univ. Montpellier.
- Cheylan, G. & L. Granjon (1985): Ecologie d'une population de rats noirs (*Rattus rattus*) à Port-Cros (Var). Méthodologie et premiers résultats obtenus sur quadrat. — *Trav. Sci. Parc nat. Port-Cros* 11: 109–131.
- Connell, J. H. (1983): On the prevalence and relative importance of interspecific competition. Evidence from field experiments. — *Am. Natur.* 122: 661–696.
- Crowell, K. L. (1973): Experimental zoogeography: introductions of mice to small islands. — *Am. Natur.* 107: 535–559.
- Crowell, K. L. (1983): Islands: insight or artifact? Population dynamics and habitat utilization in insular rodents. — *Oikos* 41: 443–454.
- Crowell, K. L. & S. L. Pimm (1976): Competition and niche shifts of mice introduced into small islands. — *Oikos* 27: 251–258.
- Darviche, D. (1978): Approche morphologique et biométrique de la biosystématique à la lumière de la génétique biochimique des populations. Application aux genres *Mus* et *Apodemus* (Mammalia, Rodentia). — Thèse Doct. 3ème cycle, Univ. Montpellier, 191 p.
- Debrot, S. & Cl. Mermod (1977): Chimiotaxonomie du genre *Apodemus* Kaup, 1829 (*Rodentia*, Muridae). — *Revue suisse Zool.* 84: 521–526.
- Delany, M. J. (1970): Variation and ecology of island population of the long-tailed field mouse (*Apodemus sylvaticus* L.). — *Symp. Zool. Soc. Lond.* 26: 283–295.
- Dueser, R. D. & J. H. Porter (1986): Habitat use by insular small mammals: relative effects of competition and habitat structure. — *Ecology* 67: 195–201.
- Felten, H. (1952): Untersuchungen zur Ökologie und Morphologie der Waldmaus (*Apodemus sylvaticus* L.) und der Gelbhalsmaus (*Apodemus flavicollis* Melchior) im Rhein-Main-Gebiet. — *Bonn. zool. Beitr.* 3: 187–206.
- Felten, H. & G. Storch (1970): Kleinsäuger von den italienischen Mittelmeer-Inseln Pantelleria und Lampedusa. — *Senckenberg. biol.* 51: 159–173.
- Filipucci, M. G. (1987): Evoluzione cromosomica e genica in micromammiferi dell'area Mediterranea (Talpidae, Gliridae, Muridae). — Ph. D. Thesis, Università di Padova, 99 p.
- Gery, J. (1962): Le problème de la sous-espèce et sa définition statistique. — *Vie & Milieu* 13: 521–540.
- Gliwicz, J. (1980): Island populations of rodents: their organization and functioning. — *Biol. Rev.* 55: 109–138.
- Granjon, L. & G. Cheylan (1988): Mécanismes de coexistence dans une guilda de muridés insulaires (*Rattus rattus* L., *Apodemus sylvaticus* L. et *Mus musculus domesticus* Ratty) en Corse; conséquences évolutives. — *Z. Säugetierk.* 53: 301–316.
- Grant, P. (1972): Interspecific competition among rodents. — *Ann. Rev. Ecol. Syst.* 3: 79–106.
- Groupe Biométrie (1988): Programmathèque Biomeco. CEPE-CNRS, route de Mende, Montpellier, 10 disquettes.
- Hallett, J. G. (1982): Habitat selection and the community matrix of a desert mammal fauna. — *Ecology* 63: 1400–1410.
- Hallett, J. G., M. A. O'Connell & R. L. Honeycutt (1983): Competition and habitat selection: test of a theory using small mammals. — *Oikos* 40: 175–181.
- Halpin, Z. T. & T. P. Sullivan (1978): Social interaction in island and mainland populations of the deer mouse, *Peromyscus maniculatus*. — *J. Mammal.* 59: 395–401.
- Hedges, S. R. (1969): Epigenetic polymorphism in populations of *Apodemus sylvaticus* and *Apodemus flavicollis* (*Rodentia*, Muridae). — *J. Zool. Lond.* 159: 425–442.

- Kahmann, H. (1969): Die Alveolenmuster der Oberkieferzahnreihe der Waldmaus, Hausratte und Hausmaus aus Populationen der großen Tyrrhenischen Inseln. — *Z. Säugetierk.* 34: 164–183.
- Kahmann, H. & J. Niethammer (1971): Die Waldmaus (*Apodemus*) auf der Insel Elba. — *Senckenberg. biol.* 52: 381–392.
- Libois, R. M. (1984): Essai synécologique sur les micromammifères d'Europe atlantique et ouest-méditerranéenne. Etude par analyse du régime alimentaire de la chouette effraie, *Tyto alba* (Scopoli). — *Cahiers Ethol. appl.* 4 (2): 1–202.
- Libois, R. M. & R. Fons (1990): Le mulot des îles d'Hyères: un cas de gigantisme insulaire. — *Vie & Milieu* 40: 217–222.
- Lidicker, W. J. (1973): Regulation of numbers in an island population of the California vole, a problem of community dynamics. — *Ecol. Monog.* 43: 271–302.
- Macarthur, R. H. & E. O. Wilson (1967): The theory of island biogeography. — Princeton, Princeton Univ. Press.
- Mayr, E., E. G. Linsley & R. L. Usinger (1953): Methods and principles of systematic zoology. — Ed. McGrawhill, New York.
- Michaux, J. (1983): Aspects de l'évolution des Muridés (Rodentia, Mammalia) en Europe sud-occidentale. — *Coll. intl. CNRS n° 330*: 195–199.
- Michaux, J. (1990): Contribution à l'étude du phénomène d'insularité: la morphologie crânienne du mulot (*Apodemus sylvaticus*). — *Mém. Lic. Sc. zool. Univ. Liège*, 48 pp. + ann. (unpublished).
- Orsini, P. (1982): Facteurs régissant la répartition des souris en Europe: intérêt du modèle souris pour une approche des phénomènes évolutifs. — Thèse 3ème cycle, Univ. Montpellier.
- Orsini, P. & G. Cheylan (1988): Les rongeurs de Corse: modifications de taille en relation avec l'isolement en milieu insulaire. — *Bull. Ecol.* 19: 411–416.
- Pacala, S. W. & J. Roughgarden (1985): Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. — *Ecology* 66: 129–141.
- Pasquier, L. (1974): Dynamique évolutive d'un sous-genre de Muridae: *Apodemus* (*Sylvaemus*). Etude biométrique des caractères dentaires de populations fossiles et actuelles d'Europe occidentale. — Thèse Doct. Univ. Montpellier, 183 p.
- Ramalhinho, M. G. & M. L. Madureira (1982): Contribution to the knowledge of *Apodemus* Kaup in Portugal (Mammalia, Rodentia). — *Arq. Museu Bocage*, 2è. sér. 9: 415–433.
- Rummel, J. D. & J. Roughgarden (1985): Effects of reduced perch-height separation on competition between two *Anolis* lizards. — *Ecology* 66: 430–444.
- Saint Girons, M. C. (1966): Etude du genre *Apodemus* Kaup, 1829, en France. I. — *Mammalia* 30: 547–600.
- Saint Girons, M. C. (1967): Etude du genre *Apodemus* Kaup, 1829, en France. II. — *Mammalia* 31: 55–100.
- Sans-Coma, V. & H. Kahmann (1977): Die Waldmaus der Pityuseninsel Formentera. — *Säugetierk. Mitt.* 19: 363–365.
- Schoener, T. W. (1983): Field experiments on interspecific competition. — *Am. Natur.* 122: 240–285.
- Sullivan, T. (1977): Demography and dispersal in island and mainland populations of the deer mouse, *Peromyscus maniculatus*. — *Ecology*, 58: 964–978.
- Tamarin, R. H. (1977): Dispersal in island and mainland voles. — *Ecology* 58: 1044–1054.
- Tamarin, R. H. (1978): Dispersal, population regulation and k-selection in field mice. — *Am. Natur.* 112: 545–555.
- Tchernov, E. (1979): Polymorphism, Size trends and Pleistocene paleoclimatic response of the subgenus *Sylvaemus* (Mammalia, Rodentia) in Israel. — *Israel J. Zool.* 28: 131–159.
- Ursin, E. (1956): Geographical variation in *Apodemus sylvaticus* and *A. flavicollis* (Rodentia, Muridae) in Europe, with special reference to Danish and Latvian populations. — *Biol. Skri. Dan. Vid. Selsk.* 8 (4): 46 p.

- Van der Straeten, E. & B. Van der Straeten-Harrie (1977): Etude de la biométrie crânienne et de la répartition d'*Apodemus sylvaticus* (L., 1758) et d'*Apodemus flavicollis* (Melchior, 1834) en Belgique. — Acta zool. pathol. Antwerpiensia 69: 169–182.
- Vigne, J. D. (1983a): Le remplacement des faunes de petits mammifères en Corse lors de l'arrivée de l'homme. — C. R. Soc. Biogéogr. 59: 41–51.
- Vigne, J. D. (1983b): Les mammifères non volants du postglaciaire de la Corse. — Thèse 3ème cycle Univ. Paris.
- Vigne, J. D. & M. C. Marival-Vigne (1985): Le rat de Corse au VIème Siècle? — Mammalia 49: 138–139.
- Vigne, J. D. & M. C. Marival-Vigne (1991): Réflexions écologiques sur le renouvellement holocène des micromammifères en Corse: les données préliminaires des fossiles du Monte di Tuda. — In: M. Le Berre & L. Le Guelte, Le Rongeur et l'Espace; Ed. Chabaud, Paris, pp. 183–192.
- Wilson, E. O. (1961): The nature of the taxon cycle in the Melanesian ant fauna. — Am. Natur. 95: 169–193.
- Williamson, M. (1981): Island populations. — Oxford Univ. Press, Oxford.

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